

Description of five new weaver ant species of *Camponotus* subgenus *Karavaievia* EMERY, 1925 (Hymenoptera: Formicidae) from Malaysia and Thailand, with contribution to their biology, especially to colony foundation

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Abstract

Five new species of *Camponotus* (*Karavaievia*) are described (workers and gynes of all species, male of *C. weissflogi*): *Camponotus* (*Karavaievia*) *aureus* DUMPERT sp.n., *C. (K.) hoelldobleri* DUMPERT sp.n., *C. (K.) maschwitzi* DUMPERT sp.n., *C. (K.) schoedli* DUMPERT sp.n., and *C. (K.) weissflogi* DUMPERT sp.n. A key is provided for determination of all the hitherto known 18 species of the subgenus *Karavaievia*.

As far as known, all *Karavaievia* species are weaver ants, producing multiple carton-silk pavilions beneath or between leaves of woody plants. All pavilions of the populous monogynous colonies contain brood and trophobiotic hemipterans. Colonies of this type of nests can only exist on plants that do not shed their foliage synchronously and frequently, i.e., on plants predominantly found in the perhumid zone. Correspondingly, most species have been recorded only from evergreen rainforests of Southeast Asia. Only few live further northwards in the semi-evergreen Dipterocarp rainforests. Colony founding queens of two species were found within nest pavilions of a canopy-living *Monomorium* species. This indicates a mode of dependent colony foundation within pavilions of carton nest building canopy ants. Possible consequences of this mode of colony-foundation for rareness and diversification of *Karavaievia* are discussed.

Key words: *Camponotus*, *Karavaievia*, weaver ants, Southeast Asia, species description, key, colony foundation, canopy.

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Introduction

Natural preformed nesting sites are rather limited in the canopy region of the tropical rainforest. By constructing free-hanging nests in this habitat, weaver ants get access to the leaf and crown region. In these ants silk of the larval labial glands is not only used by the mature larvae themselves for spinning their pupal cocoon but also for nest construction. Like weaver shuttles worker ants take large larvae with their mandibles and use the silk secreted by them to spin together leaves or to form flexible and firm carton nest walls out of particles with help of the fresh sticky silk.

Until recently four independent groups of weaver ants were known worldwide, all of them belonging to the subfamily Formicinae. Two are found in the Old World tropics (the famous genus *Oecophylla* SMITH, 1860 and many species of the genus *Polyrhachis* SMITH, 1857) and two in the New World tropics (species of the subgenera *Dendromyrmex* EMERY, 1895 and *Myrmobrachys* FOREL, 1912 of *Camponotus* MAYR, 1861) (HÖLDOBLER & WILSON 1977, SCHREMMER 1979).

In 1984 we discovered in Peninsular Malaysia near the Ulu Gombak Field Studies Centre of the University of Malaya an Old World silk-weaving *Camponotus* species which produces silk carton nests mainly beneath leaves of trees containing brood as well as trophobiotic hemipteran symbionts. This hitherto unknown species turned out to belong to the subgenus *Karavaievia* EMERY, 1925 of which two species and one subspecies had been described

from Singapore and Borneo and the Mentawai island Sipora, west of Sumatra (EMERY 1901, FOREL 1911, VIEHMEYER 1915). *Karavaievia* is thus the fifth known taxon having independently developed silk nest weaving. Since then, we discovered 15 new species, of which ten have already been described (DUMPERT 1985, DUMPERT & al. 1989, DUMPERT & al. 1995) and five will be described in this paper. Nest descriptions of the formerly discovered species indicate that all these ants use silk for pavilion nest construction.

We here additionally report for the first time on the mode of colony foundation in the subgenus *Karavaievia*, which is different from weaver ants of the genera *Polyrhachis* and *Oecophylla*, in that we show that *Karavaievia* species depend on other pavilion building canopy ants for founding their colonies. The possible influence of colony foundation mode, nesting habits and climatic influences on abundance and species diversity is discussed.

Materials and methods

Collecting sites are reported in detail in the results.

Measurements and indices:

CI Cephalic Index: $HW \times 100 / HL$
 HL Head Length: Straight-line length of head in perfect full-face view, measured from mid-point of an-

terior clypeal margin to mid-point of preoccipital margin.

- HW Head Width: Maximum width of head measured above eyes in full-face view.
- OD Ocular Diameter: Maximum diameter of compound eyes.
- OD1 Ocellar Distance 1: Straight-line length of distance between lateral ocelli measured from their inner margin.
- OD2 Ocellar Distance 2: Straight-line length of distance between one lateral to the medial ocellus measured from their inner margin.
- PW Pronotal Width: Maximum width of pronotum measured in dorsal view.
- SI Scape Index: $SL \times 100 / HW$
- SL Scape Length: Straight-line length of antennal scape, excluding basal condyle and neck.
- TL Total Length: Total outstretched length of individual, from anterior clypeal margin to gastral apex.

All measurements are expressed in millimeters. Notation of metrics as arithmetic mean \pm 1 standard deviation. Measurements were taken at $40\times$ magnification with a Leica MZ6 dissecting microscope, using a Leica micrometer. Scanning electron micrographs were taken by means of a Hitachi S 500.

Abbreviations of museums:

- CKD Klaus Dumpert Collection, Oberursel
- CSG Museo Civico di Storia Naturale Genova
- CZH Museum of Comparative Zoology at Harvard University
- FRM Forest Research Institute of Malaysia Kepong
- MNK Staatliches Museum für Naturkunde Karlsruhe
- NHB Naturhistorisches Museum Basel

Results

New descriptions by K. DUMPERT

Camponotus (Karavaievia) aureus DUMPERT sp.n.

Derivatio nominis: The name is derived from the light yellow color of the females and workers of this species.

Type material: Holotype ♀ (NHB): Thailand, Khao Sok Park, 25.XII.1998 leg. U. Maschwitz. Paratypes with same data as holotype, 14 ♂♂ (2 CZH, 2 FRM, 2 GSG, 3 MNK, 5 CKD), 10 ♀♀ (2 CZH, 2 FRM, 2 CSG, 2 MNK, 2 CKD).

Diagnosis (♂): Relatively small to fairly big animals with intermediate polymorphism in size (TL 3.9 ± 0.9). Preoccipital margin straight. Color uniformly light yellowish brown; whole body shiny.

Comparative notes (♂): The light yellowish color of *C. aureus* sp.n., is very similar to the color of *C. micragyne* DUMPERT, 1995, *C. weissflogi* sp.n., *C. belumensis* DUMPERT, 1995, and *C. asli* DUMPERT, 1989. Unlike in *C. micragyne* and *C. weissflogi* sp.n. the preoccipital margin is not concave but straight. The head of *C. aureus* sp.n. is much wider than long (CI 110.8 ± 4.8). This differs from *C. belumensis* (CI 104 ± 2) and from *C. asli* (CI 100 ± 3).

Description (♂): Measurements: Holotype: TL 4.80, HW 1.29, HL 1.13, CI 114.15, OD 0.32, SL 1.37, SI 106.2, PW 0.76. Paratypes (n = 14): TL 3.9 ± 0.9 , HW 1.23 ± 0.06 , HL 1.11 ± 0.06 , CI 110.8 ± 4.8 , OD 0.31 ± 0.012 , SL 1.25 ± 0.125 , SI 101.74 ± 9.2 , PW 0.72 ± 0.035 .

As in all *Karavaievia* species, head trapezoidal with rounded posterolateral corners; preoccipital margin straight and not at all concave. Head sides strongly convex (Fig. 1). Head wider than long (CI 114 - 115). Eyes situated behind midlength of head sides; maximum diameter 0.32 mm or nearly $0.25 \times HW$. Frontal carinae nearly straight, only slight projection behind antennal insertion. Carinae slightly divergent and extend to about midlength of head. Anterior clypeal margin slightly concave (Fig. 1). Mandibles short, lateral borders strongly curved and five subequal teeth on each masticatory border. Antennal scapes projecting beyond preoccipital margin by about one third of length. Pedicel longer than following flagellar segments; apical flagellar segments slightly thickened.

Mesosoma with deep metanotal groove and two elevated spiracles at deepest point of groove. Promesonotum, seen in profile, broadly rounded and higher than propodeum. Dorsal part of propodeum convex, descending part straight and considerably steeper (Fig. 2). Petiolar scale triangular in profile, with broad base tapering to a crest. Crest pointed when seen from front or behind.

Color uniformly light yellowish brown. Surface of head, mesosoma and gaster shiny with densely located weak punctures. Decumbent pubescence on all body parts as seen on mesosoma. Additional longer erect and suberect yellowish white hairs on all body parts.

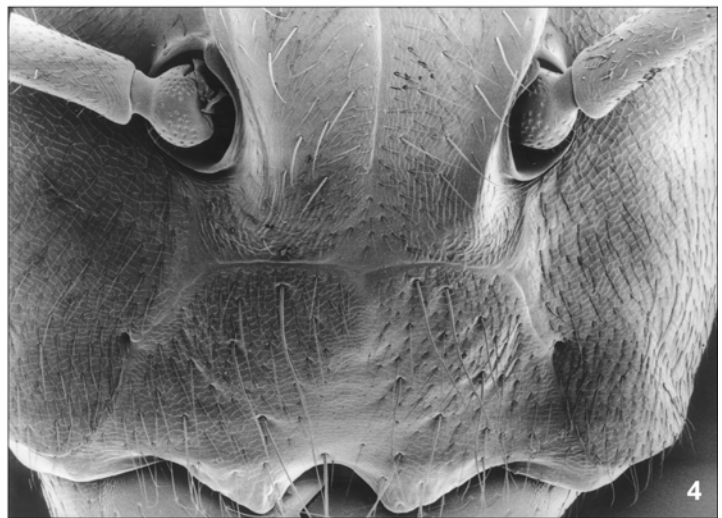
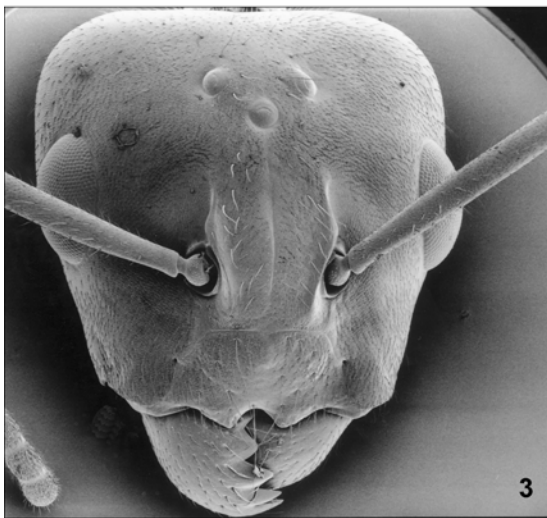
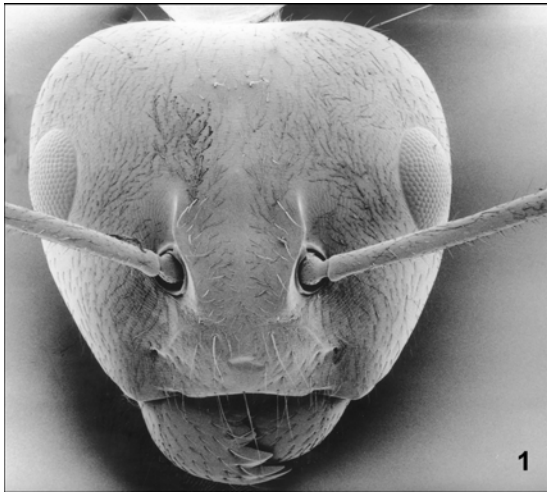
Diagnosis (♀): Frontal area as wide as high. Posterior clypeal margin without medial excision. Preoccipital margin straight. Whole animal light yellowish brown in color, head and mesosoma at least mostly opaque, scutellum also yellowish brown and shiny.

Comparative notes (♀): The frontal area of *C. aureus* sp.n. is as wide as high. In this respect *C. aureus* sp.n. is equal to *C. melanus* DUMPERT, 1995, *C. orinus* DUMPERT, 1989 and *C. gombaki* DUMPERT, 1986. The color of *C. aureus* sp.n. is different from *C. melanus* (yellowish brown instead of blackish brown). Unlike in *C. orinus* and *C. gombaki* the posterior clypeal margin of *C. aureus* sp.n. is not excised.

Description (♀): Measurements: Paratypes (n = 10): TL 11.02 ± 0.34 , HW 2.08 ± 0.07 , HL 2.08 ± 0.05 , CI 100.01 ± 4.8 , OD 0.64 ± 0.03 , SL 1.87 ± 0.14 , SI 89.90 ± 8.3 , PW 1.82 ± 0.075 .

Head as long as wide (CI 100.01 ± 4.8); sides of head nearly straight. Preoccipital margin straight. Eyes situated behind midlength of head sides. Frontal carinae extend about to midlength of head. Carinae almost straight and only slightly divergent. Anterior clypeal margin with specially pronounced semicircular excision and very strong indented edges (Figs. 3, 4). Posterior clypeal margin without median excision. Frontal area as wide as high, clearly delimited and shiny in contrast to opaque surrounding head parts (Fig. 4). Mandibles strong, rounded on outside and 5 subequal black teeth on inside. Petiolar profile with broad base tapering to transverse crest. Petiolar crest rounded when seen from front or behind.

Color uniformly light yellowish brown, gaster slightly darker. Head, mesosoma, antennae, and legs opaque, frontal area and scutellum shiny. Decumbent pubescence on all body parts as seen on the mesosoma. Additional longer erect and suberect yellowish white hairs on all body parts.



Figs. 1 - 4: *Camponotus (Karavaievia) aureus* sp.n.: (1) head of ♂; (2) mesosoma of ♂; (3) head of ♀; (4) clypeus and surrounding head parts of ♀.

***Camponotus (Karavaievia) hoelldobleri* DUMPERT sp.n.**

Derivatio nominis: The name is derived from the great myrmecologist Bert Hölldobler.

Type material: Holotype ♀ (NHB): Thailand, Khao Sok Park, 27.XII.1998, leg. U. Maschwitz. Paratypes with same data as holotype, 20 ♂♂ (2 CZH, 2 CSG, 2 FRM, 3 MNK, 11 CKD), 1 ♀ (NHB).

Diagnosis (♂): Strongly polymorphic in size (TL 4.6 ± 1.6). Petiolar scale broadly rounded when seen from front or behind. Propodeum angular on top, promesonotum rounded. In contrast to the shiny surface of nearly the whole body, clypeus strongly sculptured and opaque.

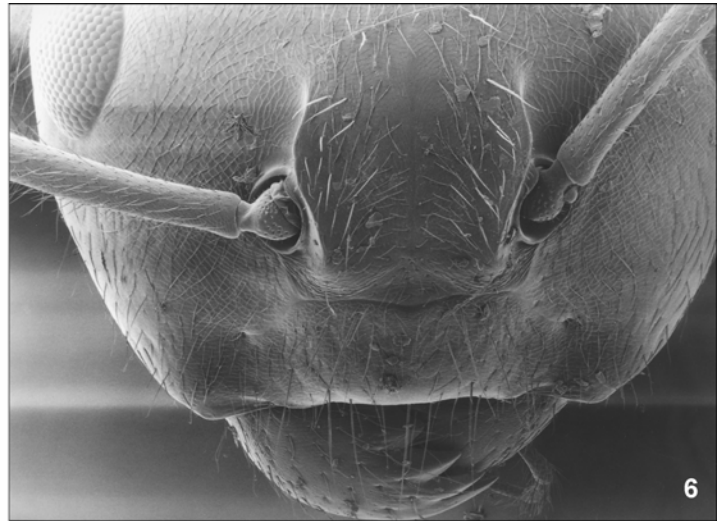
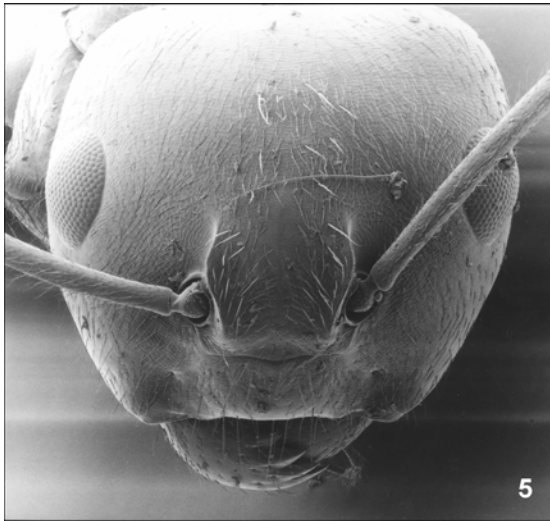
Comparative notes (♂): *C. hoelldobleri* sp.n. is dark in color like *C. melanus*. They differ from each other in the shape of the petiolar scale. The petiolar scale of *C. hoelldobleri* sp.n. is rounded when seen from front or behind instead of pointed. In this respect, *C. hoelldobleri* sp.n. differs also from *C. exsectus* EMERY, 1900, *C. overbecki* VIEHMEYER, 1916, *C. texens* DUMPERT, 1986, *C. schoedli* sp.n., and *C. maschwitz* sp.n.

Description (♂): Measurements: Holotype: TL 4.88, HW 1.36, HL 1.25, CI 108.8, OD 0.34, SL 1.33, SI 97.8,

PW 0.83. Paratypes (n = 20): TL 4.6 ± 1.6 , HW 1.44 ± 0.22 , HL 1.37 ± 0.21 , CI 105.3 ± 3.7 , OD 0.39 ± 0.012 , SL 1.54 ± 0.125 , SI 106.5 ± 11.3 , PW 0.88 ± 0.135 .

Head trapezoidal with rounded posterolateral corners; preoccipital margin concave in full face view. Head sides strongly rounded (Fig. 5). Head slightly wider than long (CI 108.8). Eyes situated behind midlength of head sides; maximum diameter 0.34 mm or $0.25 \times$ HW. Frontal carinae nearly straight with slight projection behind antennal insertion. Carinae slightly divergent and extend to less than midlength of head (Figs. 5, 6). Anterior clypeal margin straight. Mandibles short, with lateral borders strongly curved and five subequal teeth on each masticatory border. Antennal scapes projecting beyond preoccipital margin by about one third of length. Pedicel longer than following flagellar segment; apical flagellar segments slightly thickened.

Mesosoma with deep metanotal groove, with two elevated spiracles at the deepest point of the groove. Promesonotum, seen in profile, broadly rounded and higher than propodeum. Propodeal profile angular on top; descending part steeper than dorsal one (Fig. 9). Petiolar scale triangular in profile, with broad base tapering to a crest.



Figs. 5 - 8: *Camponotus (Karavaievia) hoelldobleri* sp.n.: (5) head of ♂; (6) clypeus and surrounding head parts of ♂; (7) head of ♀; (8) clypeus and surrounding head parts of ♀.

Crest pointed when seen from front or behind.

Color of mesosoma and legs uniformly light reddish brown, head and gaster darker. Surface of head, mesosoma and gaster shiny with densely located weak punctures. Clypeus strongly sculptured and opaque. Decumbent pubescence on all body parts. Additional longer erect and suberect yellowish white hairs on all parts of body.

Diagnosis (♀): Frontal area wider than high and poorly delimited. Posterior clypeal margin straight and not medially excised. Preoccipital margin strongly concave, petiolar scale seen from front or behind narrowly rounded, dark brown to black in color and shiny.

Comparative notes (♀): Similar to *C. asli* and *C. weissflogi* sp.n., the frontal area of *C. hoelldobleri* sp.n. is wider than high. Unlike *C. asli* and *C. weissflogi* sp.n. the posterior clypeal margin is not medially excised.

Description (♀): Measurements: Paratype (n = 1): TL 10.69, HW 2.67, HL 2.67, CI 100, OD 0.68, OD1 0.44, OD2 0.20, SL 2.26, SI 84.6, PW 1.78.

Head as long as wide (CI 100); sides of head nearly straight. Eyes situated behind midlength of head sides. Frontal carinae extend about to midlength of head. Carinae almost straight and slightly divergent. Anterior clypeal

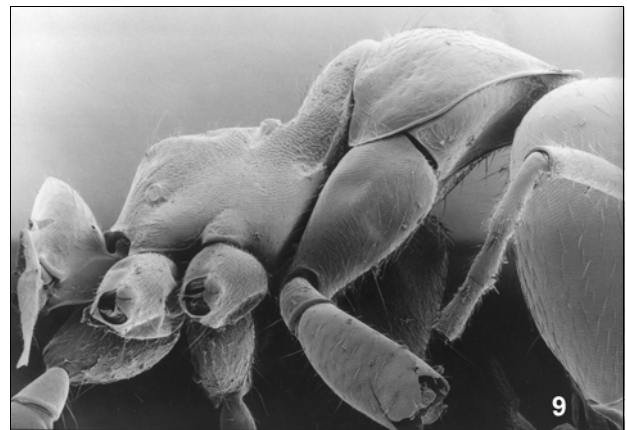
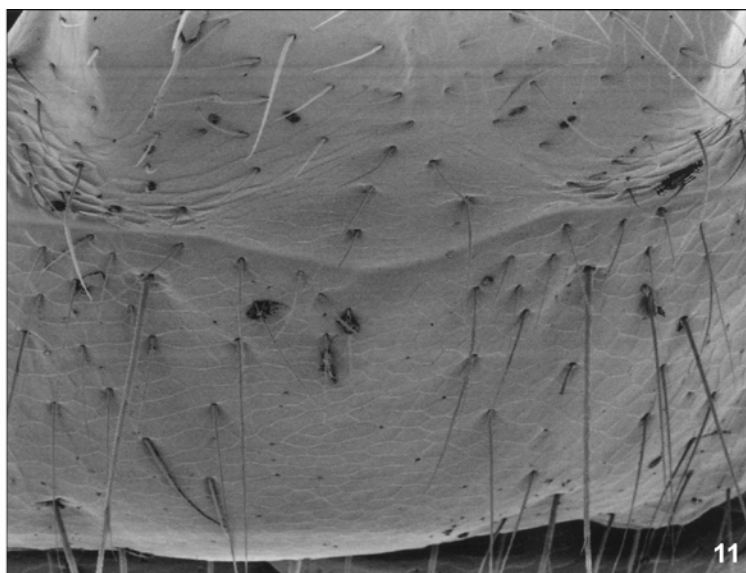
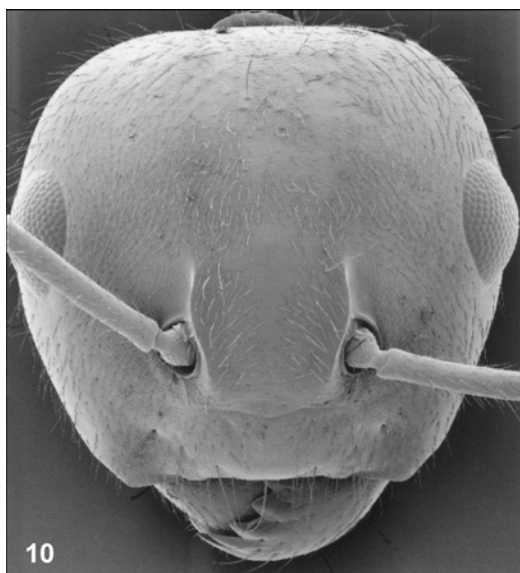


Fig. 9: *Camponotus (Karavaievia) hoelldobleri* sp.n., mesosoma of ♀.

margin with semicircular excision (Figs. 7, 8). Frontal area relatively small, wider than high, poorly delimited and strongly shiny in contrast to densely punctate surrounding head parts. Posterior clypeal margin straight and not medially excised. Mandibles strong, rounded on outside



Figs. 10 - 11: *Camponotus (Karavaievia) maschwitzi* sp.n.: (10) head of ♀; (11) clypeus and surrounding head parts of ♀.

with 5 subequal black teeth on inside. Petiolar profile with broad base tapering to dorsal transverse crest. Petiolar crest broadly rounded when seen from front or behind.

Uniformly dark brown to black in color. Head, mesosoma, antennae, and legs densely punctate and shiny. Decumbent pubescence and additional longer erect and suberect light hairs on all body parts.

***Camponotus (Karavaievia) maschwitzi* DUMPERT sp.n.**

Derivatio nominis: The name is derived from Ulrich Maschwitz, who found most of the newly described species as well as most of the previously described *Karavaievia* species.

Type material: Holotype ♀ (NHB): Malaysia, Sarawak (Borneo), near Miri, Lambir Park, 1.I.2003, leg. U. Maschwitz. Paratypes with same data as holotype, 16 ♂♂ (2 CZH, 2 FRM, 2 CSG, 3 MNK, 7 CKD), 1 ♀ (NHB).

Diagnosis (♂): Only weakly polymorphic in size (TL 3.6 ± 0.4). Head, mesosoma and legs reddish brown, gaster blackish. Head as long as wide. Preoccipital margin straight. Petiolar scale pointed when seen from front or behind. Clypeus as much shiny as the rest of the head.

Comparative notes (♂): The head of this species is as long as wide. Other species with CI values of 100 or less than 100 are *C. exsectus*, *C. overbecki*, *C. texens*, and *C. schoedli* sp.n. Within this group the species differ considerably in their color with the exception of *C. schoedli* sp.n. and *C. maschwitzi* sp.n. Both species have also the same color (head, antennae and mesosoma reddish brown, gaster black). Workers of these species cannot be distinguished from each other. Gynes of these species, however, differ so much that there is enough reason to put them into two different species.

Description (♂): Holotype: TL 3.95, HW 1.21, HL 1.17, CI 103.4, OD 0.32, SL 1.29, SI 106.6, PW 0.72. Paratypes (n = 16): TL 3.6 ± 0.4 , HW 1.16 ± 0.09 , HL 1.15 ± 0.1 , CI 100.6 ± 3.4 , OD 0.3 ± 0.02 , SL 1.33, SI 115.4 ± 2.6 , PW 0.71 ± 0.04 .

Head trapezoidal with rounded posterolateral corners; preoccipital margin straight in full face view. Head sides

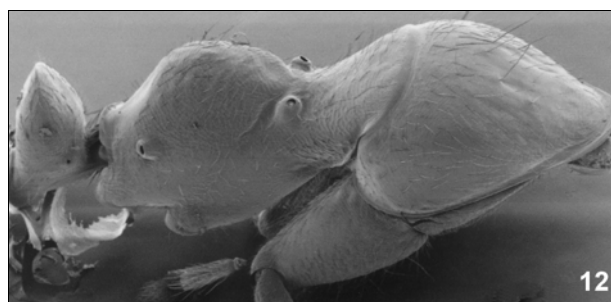
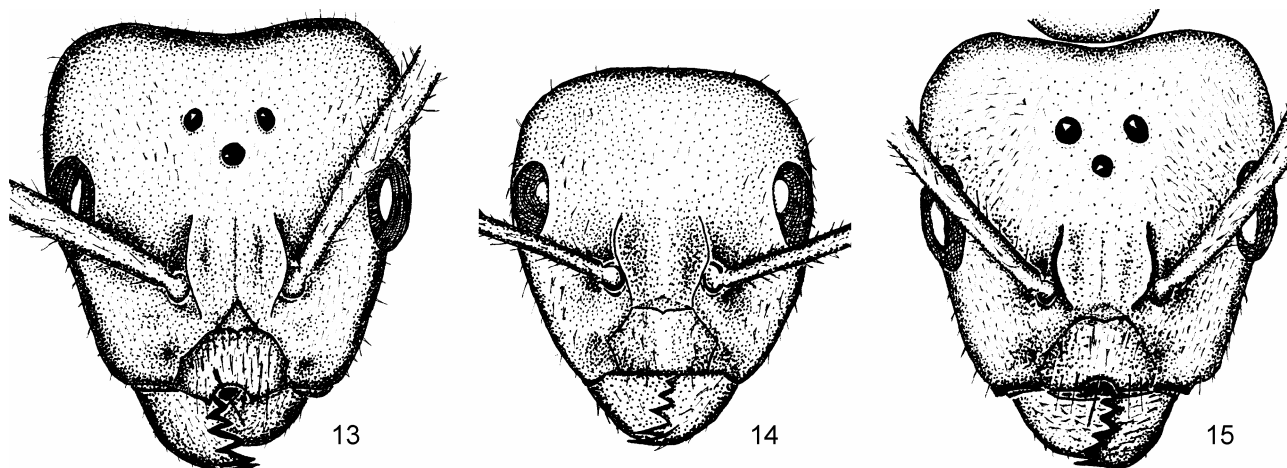


Fig. 12: *Camponotus (Karavaievia) maschwitzi* sp.n., mesosoma of ♀.

strongly rounded (Fig. 10). Head as long as wide (CI 100.6 ± 3.4). Eyes situated behind midlength of head sides, maximum diameter 0.32 mm ($0.26 \times$ HW). Frontal carinae nearly straight with slight projection behind antennal insertion. Carinae slightly divergent and extend to less than midlength of head (Fig. 10). Frontal area weakly delimited, anterior clypeal margin slightly convex (Fig. 11). Mandibles short, with lateral borders strongly curved and five subequal teeth on each masticatory border. Antennal scapes projecting beyond preoccipital margin of about one third their length. Pedicel longer than the following flagellar segment; apical flagellar segments slightly thickened.

Mesosoma with deep metanotal groove, with two elevated spiracles at the deepest point of the groove. Promesonotum, seen in profile, broadly rounded; propodeum slightly higher than promesonotum and nearly as rounded. Dorsal and descending parts of propodeum straight; descending part steeper than dorsal one (Fig. 12). Petiolar scale triangular in profile, with a broad base tapering to a dorsal crest. Crest pointed when seen from front or behind.

Color of head and mesosoma dark reddish brown, gaster blackish brown; promesonotum and legs lighter. Surface of head, mesosoma and gaster shiny with densely located distinct punctures especially on gaster. Clypeus as



Figs. 13 - 15: Head, frontal view of (13) *Camponotus (Karavaievia) maschwitzi* sp.n., ♀; (14) *C. (K.) schoedli* sp.n., ♂; (15) *C. (K.) schoedli* sp.n., ♀.

much shiny as rest of head. Decumbent pubescence and additional longer erect and suberect yellowish white hairs on all body parts.

Diagnosis (♀): Frontal area as wide as high and clearly delimited from surrounding head parts. Anterior clypeal margin medially excised. Petiolar scale excised while seen from front or behind. Wholly black, except front parts of head, pronotum and legs. Gaster and legs shiny, rest of body opaque.

Comparative notes (♀): The frontal area of this species is as wide as high and clearly delimited. The frontal area of *C. schoedli* sp.n., however, is much wider than high and poorly delimited. Different from that of *C. schoedli* sp.n., the petiolar scale of *C. maschwitzi* sp.n. is distinctly excised when seen from front or behind. Also the colors are quite different: The gyne of *C. schoedli* sp.n. is blackish brown with reddish brown legs and antennae, but the gyne *C. maschwitzi* sp.n. has head and mesosoma dark reddish brown, gaster blackish brown, and promesonotum and legs lighter.

Description (♀): Measurements: Paratype (n = 1): TL 10.15, HW 2.43, HL 2.33, CI 104.3, OD 0.72, SL 2.18, SI 89.7, PW 1.85, OD 0.39, OD1 0.16, OD2 0.2.

Head nearly as long as wide (CI 104.3). Preoccipital margin strongly concave, posterolateral corners rounded. Sides of head slightly rounded. Eyes situated behind midlength of head sides. Frontal carinae extend to about midlength of head. Carinae almost straight and slightly divergent. Anterior clypeal margin with semicircular excision. Posterior clypeal margin medially excised (Fig. 13). Frontal area as wide as high, shiny and clearly delimited from densely punctate surrounding head parts. Mandibles strong, rounded on outside with 5 subequal black teeth on inside. Petiolar profile with broad base tapering to a transverse crest. Petiolar crest distinctly excised when seen from front or behind.

Head and body uniformly black in color. At most, small parts of head, mesosoma, antennae or legs lighter. All body parts densely punctate, shiny and covered with decumbent pubescence and additional longer erect and suberect hairs.

Camponotus (Karavaievia) schoedli DUMPERT sp.n.

Derivatio nominis: The name is derived from the recently died great myrmecologist Stefan Schödl.

Type material: Holotype ♂ (NHB): Thailand, Khao Sok Park, 27.XII.1998, leg. U. Maschwitz. Paratype with same data as holotype, 1 ♀ (NHB).

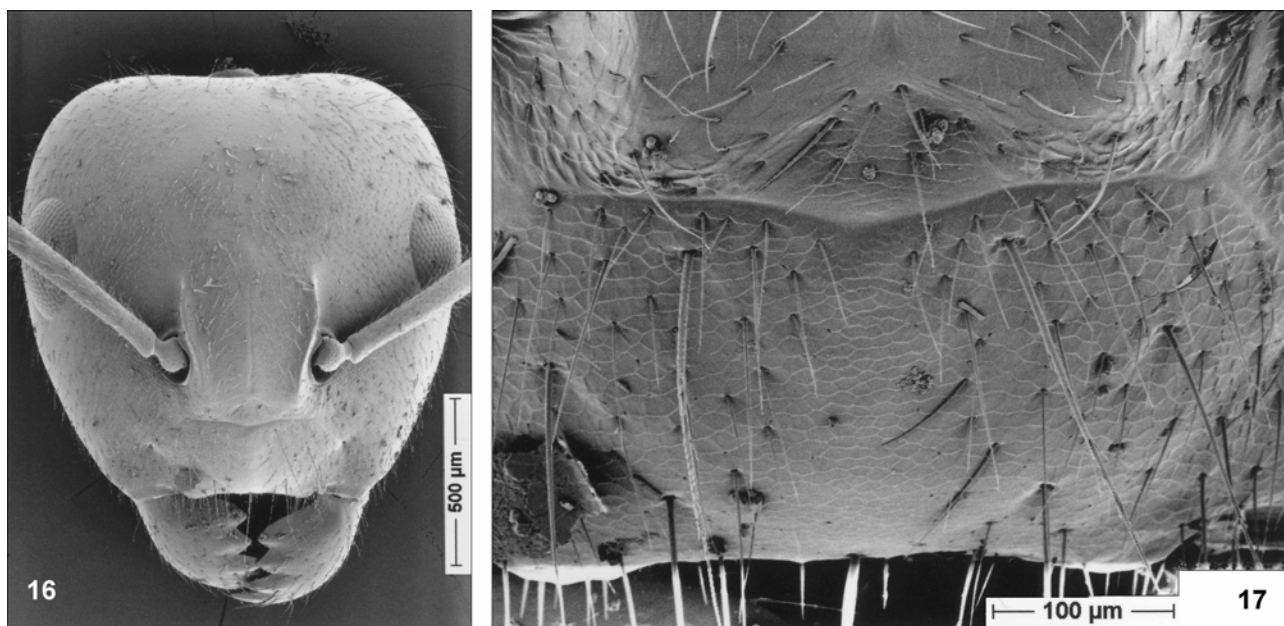
Diagnosis (♂): Head, mesosoma and legs reddish brown, gaster blackish. Head as long as wide. Preoccipital margin straight. Petiolar scale pointed when seen from front or behind. Clypeus as shiny as the rest of the head.

Comparative notes (♂): The head of this species is as long as wide. Other species with CI values of 100 or less than 100 are *C. exsectus*, *C. overbecki*, *C. texens* and *C. maschwitzi* sp.n.. Within this group the species differ considerably from each other in their color with the exception of *C. schoedli* sp.n. and *C. maschwitzi* sp.n. Both species have the same color: head, antennae and mesosoma reddish brown, gaster black. Workers of these species cannot be distinguished from each other. Gynes of these species, however, differ so much that there is enough reason to put them into two different species.

Description (♂): Measurements: Holotype: TL 4.0, HW 1.05, HL 1.05, CI 100, OD 0.28, SL 1.27, SI 120.9, PW 0.65.

Head trapezoidal with rounded posterolateral corners; preoccipital margin straight in full face view. Head sides strongly rounded (Fig. 14). Head as long as wide (CI 100.6 ± 3.4). Eyes situated behind midlength of head sides, maximum diameter 0.32 mm or $0.26 \times$ HW. Frontal carinae nearly straight with slight projection behind scapal insertion. Carinae slightly divergent and extend to less than midlength of head (Fig. 14). Anterior clypeal margin straight. Mandibles short, with lateral borders strongly curved and five subequal teeth on each masticatory border. Antennal scapes projecting beyond preoccipital margin by about one third of length. Pedicel longer than following flagellar segment; apical flagellar segments slightly thickened.

Mesosoma with deep metanotal groove and two elevated spiracles at deepest point of groove. Promesonotum,



Figs. 16 - 17: *Camponotus (Karavaievia) weissflogi* sp.n.: (16) head of ♀; (17) clypeus and surrounding head parts of ♀.

seen in profile, broadly rounded; propodeum slightly higher than promesonotum and nearly as rounded. Dorsal and descending parts of propodeum straight; descending part steeper than dorsal part. Petiolar scale triangular in profile with broad base tapering to dorsal transverse crest. Crest pointed when seen from front or behind.

Color of head and mesosoma dark reddish brown, gaster blackish brown; promesonotum and legs lighter. Surface of head, mesosoma and gaster shiny with dense distinct punctures especially on gaster. Clypeus as shiny as rest of head. Decumbent pubescence and additional longer erect and suberect yellowish white hairs on all body parts.

Diagnosis (♀): Frontal area much wider than high and poorly delimited. Anterior clypeal margin medially excised. Preoccipital margin concave. Petiolar scale pointed when seen from front or behind. Wholly reddish or blackish brown.

Comparative notes (♀): The frontal area of this species is much wider than high and poorly delimited. The frontal area of *C. maschwitzi* sp.n. is as wide as high and clearly delimited. Different from *C. schoedli* sp.n., the petiolar scale of *C. maschwitzi* sp.n. is distinctly excised when seen from front or behind. Also the colors are quite different, in *C. schoedli* sp.n. being blackish brown with reddish brown legs and antennae, in *C. maschwitzi* sp.n. on the other hand, with head and mesosoma dark reddish brown, gaster blackish brown, and promesonotum and legs lighter.

Description (♀): Measurements: Paratype (n = 1): TL 9.5, HW 2.35, HL 2.25, CI 104.4, OD 0.73, SL 1.98, SI 84.3, PW 1.74.

Head nearly as long as wide (CI 104.4). Preoccipital margin concave, posterolateral corners rounded. Sides of head nearly straight. Eyes situated behind midlength of head sides. Frontal carinae extend about to midlength of head. Carinae almost straight and only slightly divergent (Fig. 16). Anterior clypeal margin with semicircular excision. Frontal area much wider than high and poorly de-

limited (Fig. 17). Posterior clypeal margin medially excised. Mandibles strong, rounded on outside and with 5 subequal teeth on inside. Petiolar profile with broad base tapering to transverse crest. Petiolar crest pointed when seen from front or behind.

Color of hind parts of head, pro- and mesonotum, upper parts of legs and antennal flagellum reddish brown, rest of body blackish brown in color. All body parts densely punctate and shiny and covered with decumbent pubescence, additional longer erect and suberect hairs.

Camponotus (Karavaievia) weissflogi DUMPERT sp.n.

Derivatio nominis: The name is derived from Andreas Weissflog, who was the first to find a colony of this species.

Type material: Holotype ♀ (NHB): W Malaysia, Sungai Tekala Park, 13.V.1995, leg. A. Weissflog. Paratypes with the same data as holotype, 14 ♂♂ (2 CZH, 2 FRM, 2 CSG, 3 MNK, 5 CKD), 5 ♀♀ (1 CZH, 1 FRM, 1 CSG, 1 MNK, 1 CKD), 1 ♂ (NHB).

Diagnosis (♂): Weakly polymorphic (TL 4.6 ± 0.4). Light yellowish brown and shiny. Preoccipital margin strongly concave. Head only slightly wider than long.

Comparative notes (♂): The light yellowish color of *C. weissflogi* sp.n. is similar to the color of *C. aureus* sp.n., *C. micragyne*, *C. belumensis*, and *C. asli*. Unlike as in *C. aureus* sp.n., *C. micragyne*, *C. belumensis*, and *C. asli*, the preoccipital margin is not straight or slightly concave, but strongly concave like the upper part of a heart.

Description (♂): Measurements: Holotype: TL 4.55, HW 1.70, HL 1.62, CI 104.9, OD 0.36, SL 1.37, SI 80.58, PW 0.105. Paratypes (n = 14): TL 4.6 ± 0.4 , HW 1.32 ± 0.06 , HL 1.26 ± 0.08 , CI 103.8 ± 4.2 , OD 0.35 ± 0.01 , SL 1.35 ± 0.11 , SI 102.5 ± 4.5 , PW 0.81 ± 0.02 .

Head trapezoidal with rounded posterolateral corners; preoccipital margin strongly concave in full face view. Head sides rounded (Fig. 16). Head slightly wider than long (CI 103.8 ± 4.2). Eyes situated behind midlength of head sides, diameter 0.36 mm ($0.21 \times$ HW). Frontal cari-

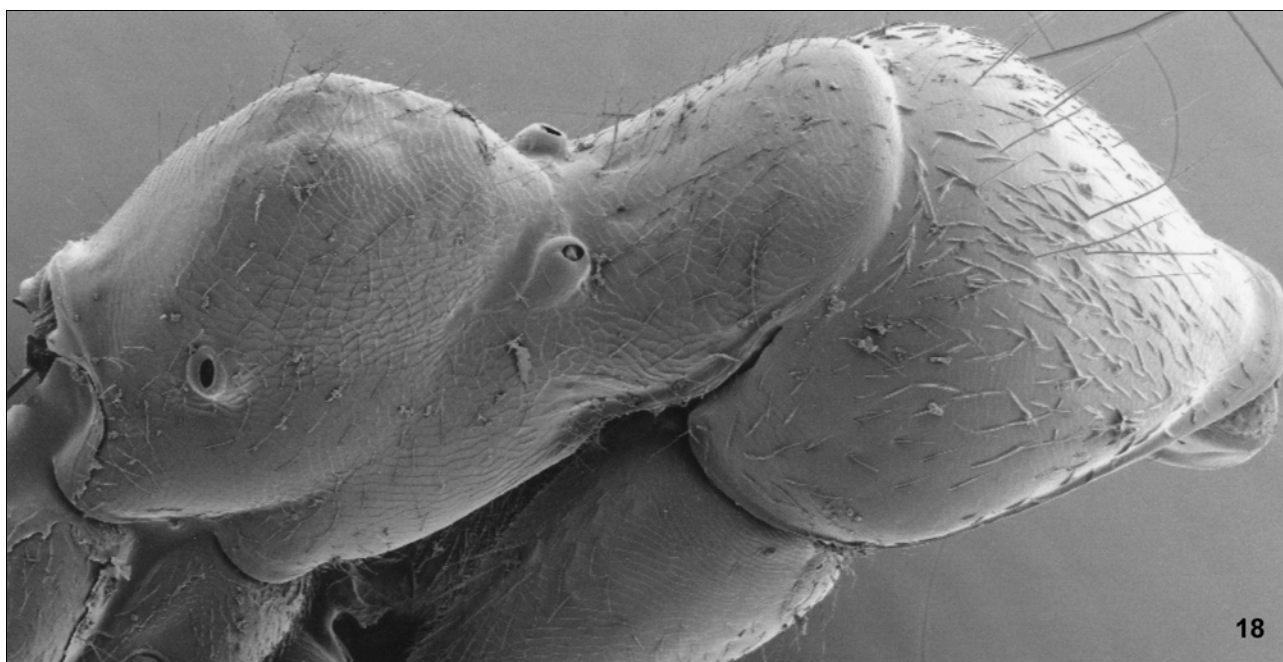


Fig. 18: *Camponotus* (*Karavaievia*) *weissflogi* sp.n., mesosoma of ♀.

nae nearly straight with slight projection behind antennal insertion. Carinae slightly divergent and extend to less than midlength of head. Frontal area clearly delimited, anterior clypeal margin slightly concave (Figs. 16, 17). Mandibles short, with lateral borders strongly curved and five subequal teeth on each masticatory border. Antennal scapes projecting beyond preoccipital margin by about one third of length. Pedicel longer than following flagellar segment; apical flagellar segments slightly thickened.

Mesosoma with deep metanotal groove, with two elevated spiracles at deepest point of groove (Fig. 18). Promesonotum, seen in profile, broadly rounded and not as high as propodeum. Propodeal profile rounded on top; dorsal and descending parts straight, descending part steeper than dorsal one (Fig. 18). Petiolar scale triangular in profile, with broad base tapering to a crest. Crest pointed when seen from front or behind.

Color of mesosoma and legs uniformly light yellowish brown. Surface of head, mesosoma, and gaster shiny. Decumbent pubescence on all body parts. Additional longer erect and suberect yellowish white hairs on all parts of body.

Diagnosis (♀): Frontal area slightly wider than high and poorly delimited. Head pale yellowish brown, mesosoma, legs, and gaster darker (at least partly). Whole body shiny. Preoccipital margin strongly concave; petiolar scale broadly rounded while seen from front or behind.

Comparative notes (♀): The posterior clypeal margin of *C. weissflogi* sp.n. is medially excised. This is also the case in *C. asli*. Both species differ, however, in their color, which is uniformly reddish brown in *C. asli*, but yellowish brown on head, and darker on mesosoma, legs, and gaster in *C. weissflogi* sp.n.

Description (♀): Measurements: Paratypes (n = 5): TL 9.34 ± 0.23, HW 2.13 ± 0.01, HL 2.16 ± 0.08, CI 98.6 ± 2.9, OD 0.68 ± 0.02, SL 1.91 ± 0.04, SI 89.2 ± 1.56, PW 1.65 ± 0.03.

Head on average slightly longer than wide (CI 98.6 ± 2.9); sides of head nearly straight. Preoccipital margin strongly concave, posterolateral corners broadly rounded (Fig. 19). Eyes situated behind midlength of sides of head. Frontal carinae extend to about midlength of head. Carinae almost straight and slightly divergent. Anterior clypeal margin with semicircular excision (Figs. 19, 20). Frontal area wider than high, relatively small and shiny, but not clearly delimited from shiny rest of head. Mandibles strong, rounded on outside, and with 5 subequal black teeth on inside. Petiolar profile with broad base tapering to transverse crest. Petiolar crest broadly rounded when seen from front or behind.

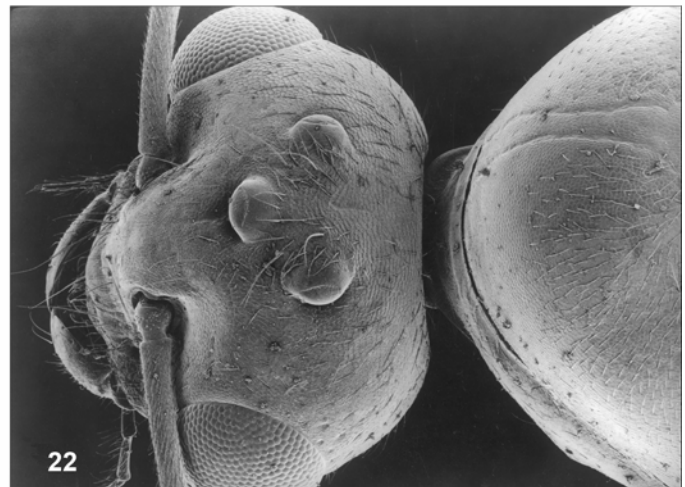
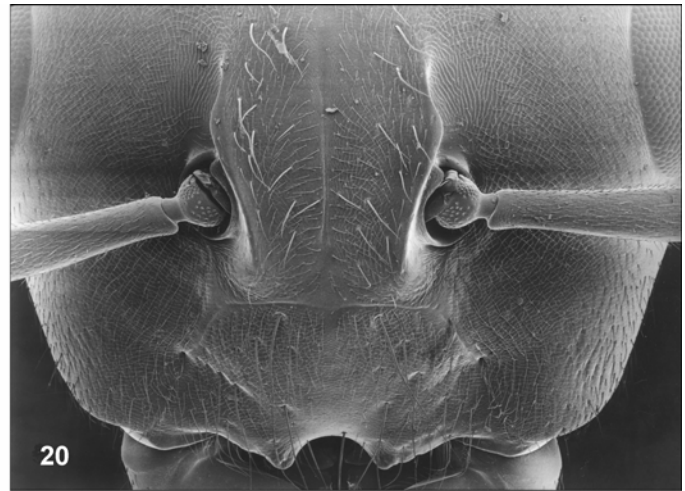
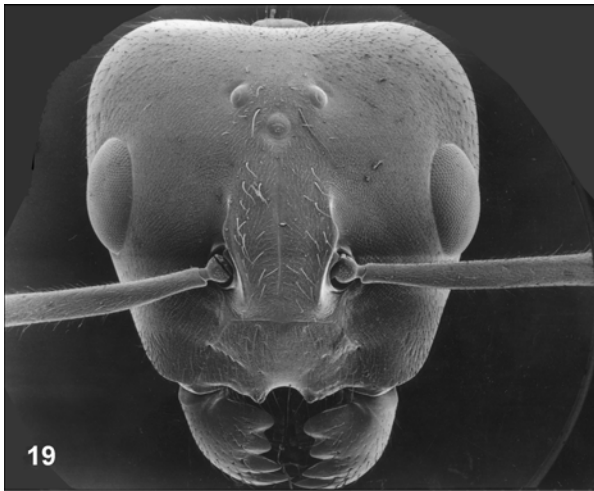
Head pale yellowish brown, mesosoma, legs, and gaster darker (at least partly). Head and body shiny. Decumbent pubescence and additional longer erect and suberect light hairs on all body parts.

Diagnosis (♂): Head as long as wide. Clypeus wider than long (0.35 × 0.2 mm). Front head lighter than the rest of body. Scutellum dark brown and shiny.

Comparative notes (♂): The head of *C. weissflogi* sp.n. is as wide as long. This is also the case in *C. gentingensis* DUMPERT, 1995 and *C. texens*. Unlike in *C. gentingensis* and *C. texens*, the front part of *C. weissflogi* sp.n. is distinctly lighter than the rest of the head.

Description (♂): Measurements: Paratype (n = 1): TL 5.3, HW 0.97, HL 0.97, CI 100, OD 0.42, SL 0.93, SI 104.3, PW 1.14.

Head trapezoidal and as long as wide (CI 100); preoccipital margin strongly convex with protruding ocelli (Figs. 21, 22) and prominent convex eyes, extending to upper end of head sides (Fig. 21). Anterior clypeal margin straight. Frontal carinae short and sinuate, reaching back to about midlength of head. Maximum diameter of eyes 0.42 mm and less than half head width. Scapes long, projecting beyond preoccipital margin of head by about half of length. Pedicel expanded at its distal end and thicker



Figs. 19 - 22: *Camponotus (Karavaievia) weissflogi* sp.n.: (19) head of ♀; (20) clypeus and surrounding head parts of ♀; (21) head of ♂, frontal; (22) head of ♂, dorsal.

than following flagellar segments. Propodeal profile rounded with convex dorsal and weakly convex descending part. Petiolar scale triangular in profile, with broad base tapering to a crest. Crest with deep median excision.

Color uniformly dark yellowish brown, front head lighter, scutellum, legs and parts of gaster dark brown. Except shiny scutellum and slightly shiny gaster, cuticle more or less opaque. Decumbent pubescence and additional longer erect and suberect hairs on whole body.

Keys to the known species of the subgenus *Karavaievia* by K. DUMPERT

Workers

- 1 Head and mesosoma shiny. 2
- Head and mesosoma opaque. 10
- 2 Body slender; decumbent pubescence lacking. Head distinctly longer than wide (CI 90.4 ± 2.4). *C. striatipes* DUMPERT, 1995
- More robust, decumbent pubescence present. 3
- 3 Yellow or lightly yellowish brown in color. 4
- Darker in color. 7

- 4 Head wider than long (CI 107 ± 1.6). 5
- Head not that much wider than long (CI 104 or below). 6
- 5 Preoccipital margin slightly concave... *C. micragyne*
- Preoccipital margin strongly concave, like upper part of a heart. *C. weissflogi* sp.n.
- Preoccipital margin straight. *C. aureus* sp.n.
- 6 Smaller (HL 1.06 ± 0.04 ; HW 1.08 ± 0.05).
..... *C. belumensis*
- Larger (HL 1.21 ± 0.07 ; HW 1.21 ± 0.06). ... *C. asli*
- 7 Petiolar scale broadly rounded when seen from front or behind. *C. hoelldobleri* sp.n.
- Petiolar scale pointed when seen from front or behind. 8
- 8 Head wider than long (CI 104 ± 2). *C. melanus*
- Head longer than wide or as long as wide (CI equal or less than 100). 9
- 9 Uniformly dirty yellow, anterior parts of head and gaster lighter; gaster with darker segment borders. *C. exsectus*

- Head, mesosoma, and legs reddish brown, gaster blackish brown with lighter brown segment borders; apical flagellum and front of head yellow. *C. overbecki*
- Head, mesosoma, scapes and legs dark brown; gaster, petiole, apical antennal flagellum and front of head reddish. *C. texens*
- Head, antennae, legs, and mesosoma reddish brown, gaster black.
..... *C. schoedli* sp.n. and *C. maschwitz* sp.n.
- 10 Large (HL and HW 1.4 - 1.5 mm on average). 11
- Smaller (HL and HW less than 1.4 mm). 12
- 11 Head, gaster, and legs uniformly brown, mesosoma yellowish, scapes and basal antennal segments dark brown. *C. gentingensis*
- Head and gaster dark brown, mesosoma reddish to dark brown. *C. orinus*
- 12 Legs uniformly dark to blackish brown.
..... *C. nigripes* DUMPERT, 1995
- Legs lighter in color. 13
- 13 Uniformly dirty yellowish brown; tarsi, apical antennal flagellum and front of head reddish. ..
..... *C. dolichoderoides* FOREL, 1911
- Head and mesosoma reddish brown, gaster dark brown. *C. gombaki*

Gynes

- 1 Petiolar scale blunt in lateral view. *C. exsectus*
- Petiolar scale acute in dorsal view. 2
- 2 Anterior clypeal margin with only a very small median excision; legs brown with three broad white bands. *C. striatipes*
- Anterior clypeal margin with strong semicircular excision. 3
- 3 Total length about 7 mm. *C. micragyne*
- Total length more than 9 mm. 4
- 4 Frontal area much wider than high and poorly delimited. *C. schoedli* sp.n.
- Frontal area only slightly wider than high or as wide as high. 5
- 5 Frontal area only slightly wider than high and poorly delimited. 6
- Frontal area as wide as high. 8
- 6 Anterior clypeal margin without medial excision. *C. hoelldobleri* sp.n.
- Anterior clypeal margin with slight medial excision. 7
- 7 Uniformly reddish brown, scutellum and metanotum darker. *C. asli*
- Head and mesosoma light yellowish brown.
..... *C. weissflogi* sp.n.
- 8 Anterior clypeal margin without medial excision. 9
- Anterior clypeal margin more or less excised. 10

- 9 Uniformly blackish brown in color. *C. melanus*
- Head, mesosoma and legs yellowish brown in color, gaster darker. *C. aureus* sp.n.
- 10 Anterior clypeal margin with strong medial excision. 11
- Anterior clypeal margin only slightly medially excised. 12
- 11 Uniformly black or blackish brown in color. ..
..... *C. orinus*
- Head, mesosoma and legs reddish brown, gaster darker. *C. gombaki*
- 12 Petiolar scale distinctly excised when seen from front or behind. *C. maschwitz* sp.n.
- Petiolar scale not excised. 13
- 13 Head and mesosoma shiny; mesosoma strongly sculptured, showing stripe-like structures.
..... *C. belumensis*
- Head and mesosoma opaque, mesosoma without stripe-like structures. *C. gentingensis*

Males (♂♂ of some species unknown.)

- 1 HW < 0.9 mm. 2
- HW > 0.9 mm. 5
- 2 Head wider than long. *C. gentingensis*
- Head longer than wide. 3
- 3 Pronotum with two dark stripes. *C. striatipes*
- Pronotum without dark stripes. 4
- 4 Scutellum dark brown. *C. asli*
- Scutellum yellowish brown. *C. melanus*
- 5 HW nearly 1.1 mm and more. *C. orinus*
- HW between 0.9 and 1.05 mm. 6
- 6 Head wider than long. 7
- Head nearly as wide as long. 8
- 7 CI 115, scutellum shiny. *C. micragyne*
- CI 108, scutellum opaque. *C. gombaki*
- 8 Front part of head lighter than rest of head.....
..... *C. weissflogi* sp.n.
- Front part of head not lighter than rest of head. 9
- 9 Uniformly reddish brown in color. *C. gentingensis*
- Head and mesosoma blackish brown, gaster yellowish brown. *C. texens*

Contribution to the biology of *Karavaievia*

Collection sites and nest descriptions

The colony of *C. (K.) aureus* sp.n. was found in the Khao Sok National Park (Peninsular Thailand) on two neighboring trees, both about 4 m in height. The colony consisted of 94 inhabited pavilions. Most of them were woven on the undersides of leaves while less than 1 % was built between leaves. All pavilions were built of silk and carton material, had only one chamber and one entrance with diameters of about 2 mm. Inside all occupied pavilions tropho-

bionts were found, belonging to one (unidentified) coccid species. The mean length of the pavilions was 6.49 cm and the mean width 1.48 cm, the ratio of nest length to nest width: 4.3 to 1. The interior floor of the pavilions was not covered with silk. In addition to many adult workers, we found one functional queen, 15 winged females, numerous eggs, larvae, and pupae (not enclosed in cocoons), but no males. Ten females and 15 workers were taken for the description.

A single colony of *C. (K.) hoelldobleri* sp.n. was detected in the Khao Sok National Park (Thailand) on an unidentified tree about 5 m in height. The colony consisted of 145 pavilions concentrated on three separate branches with a mean length of 10.47 cm and a mean width of 1.66 cm, ratio of nest length to nest width: 6.3 to 1. All pavilions were built on the undersides of leaves. The interior floor of the pavilions was covered with a thin silk layer. In addition to numerous adult workers, we found two wingless queens and a few larvae, but no other sexuals and no pupae. Both females and 20 workers were taken for the description.

In the case of *C. (K.) schoedli* sp.n. we found two initial colonies in the Khao Sok National Park. These initial colonies consisted of one pavilion, each. One of them was 3.5 cm long and 1 cm wide, the other 4 cm long and 1.2 cm wide and each had one entrance. Both consisted mainly of hairy material, which is highly typical for *Monomorium* sp. (WEISSFLOG 2001). Each pavilion contained some silk and was occupied by some coccids. One of the pavilions was inhabited by one queen, three small workers and one pupa covered by a very thin cocoon. The other one contained one wingless queen, three small workers, some larvae and one pupa also covered by a very thin cocoon. Both of these colonies contained the same species of coccid as we found in the *Monomorium* colonies. Close to the pavilions we found another *Monomorium* colony. The single pavilion of this colony contained brood and coccid trophobionts. Apparently the *C. (K.) schoedli* sp.n. queens had taken over pavilions of this *Monomorium* sp. colony.

Camponotus (K.) maschwitzi sp.n. was found during an excursion to Borneo (Sarawak, near Miri, Lambir Park). The colony was situated in a dense primary forest on a small tree, 3.5 m in height. It consisted of 12 pavilions which were built on the undersides of leaves and distributed over eleven branches of this tree. The pavilions of this species are extremely long and narrow. The mean length of all present pavilions was 8.5 cm and the mean width was 0.96 cm, constituting a ratio of length to width of 8.85 to 1. All pavilions had only one chamber and one entrance. The interior floor of each pavilion was covered with a thin silk layer. The nest contained (unidentified) coccids as trophobionts. The colony consisted of one active queen, many worker ants and brood but no other sexuals. Some of the pupae had a thin cocoon whereas some others had no cocoon at all. The queen and 20 workers were taken for the description.

The colony of *C. (K.) weissflogi* sp.n. was found in West Malaysia in the Sungai Tekala Park (Selangor, Negeri Sembilan). The approximately 200 pavilions of this species were evenly distributed on three adjacent trees at heights of 2 - 10 m. Of the pavilions, 136 (68 %) were located between living leaves, held together by a flexible silken wall with approximately 1 cm distance to the leaf mar-

gin. They were oval shaped (12 × 8 cm) and roughly resembled the size and form of the leaves. The remaining pavilions were built on the undersides of leaves and attached to the midrib (length 5 - 12 cm, width 3 - 5 cm). All pavilions showed only a single entrance hole. The use of larval silk as building material was restricted to the outer nest walls; besides silk the ants used wooden particles and (rarely) insect remains (e.g., cuticles) for nest construction. The inner nesting space was never subdivided by additional walls and neither the floor nor roof was covered with silk. The nests were inhabited by some thousand workers, different stages of brood and many sexuals. Trophobiotic coccids were located inside all pavilions. In the near vicinity (5 m) of the *C. (K.) weissflogi* sp.n. colony two independent colonies of *Monomorium* were located on single trees in 2 - 3 m height and containing about 20 carton nest pavilions (WEISSFLOG 2001).

Colony foundation in *C. (K.) melanus*

In Borneo a *C. (K.) melanus* queen without brood was the sole ant in one of five *Monomorium* sp. pavilions (12.3 cm length and 1.1 cm width), with the other four pavilions still being occupied by their original owners. The *C. (K.) melanus* containing pavilion was built out of leaf hairs in the typical nest building mode of *Monomorium* and contained no silk.

The coccids located in both the single nest occupied by the *C. (K.) melanus* queen and inside the four detected *Monomorium* pavilions, belong to the same species (*Coccus hesperidius* LINNAEUS, 1758). Average measurements of the four *Monomorium* pavilions were 12.3 cm × 1.1 cm × 0.3 cm. It is noticeable that the single nest taken over by *C. (K.) melanus* was enlarged in width and height (4 cm × 1.5 cm) apparently to be more suitable for the much larger *Karavaievia* inhabitants. Microscopic structure of the nest walls indicated that this enlargement was done by the tiny *Monomorium* workers (WEISSFLOG 2001). These findings seem to represent the earliest stage of colony foundation of a *Karavaievia* colony. In contrast, in *C. (K.) micragyne*, which is known from West Malaysia and Sumatra, we came upon a progressive stage of colony establishment which will be described here in more detail.

Relation of *C. (K.) micragyne* with *Monomorium* sp.

In North Sumatra (Ketambe, G. Leuser National Park) we found a huge colony (> 100 pavilions) of *C. (K.) micragyne* which shared some of its pavilions with a *Monomorium* species. Beside "typical" *Karavaievia* nest pavilions located under leaves and made with the help of larval silk, the colony occupied partly the nest pavilions of the *Monomorium* species. Altogether we found three types of nest pavilions in this *Karavaievia* colony, in close proximity to one another, even on the same leaf:

(I) Wide, oval shaped nest pavilions (max. length: 10 cm, width: 5 cm, height: 1.5 cm), made mainly from larval silk riddled with relatively coarse wooden particles and inhabited only by *C. (K.) micragyne*.

(II) Narrow, tube shaped nests (max. length: 9 cm, width: 1.5 cm, height: 1.5 cm), built laterally on nerves of leaves, made from fine plant trichomes derived from the nest leaves, with only the inner surface of the nest walls covered (irregularly) with silk. Inhabited solely by *C. (K.) micragyne* (workers, alates, brood).

(III) Same architecture as type (II), however, colonized by *C. (K.) micragyne* workers with brood and alate females and additionally by the *Monomorium* species (queen, workers, brood). Though silk was used for covering the inner surfaces of walls, these nests were not divided into separate chambers. Both species were aggregated on opposed sides of the nest without any sign of aggressiveness. Only when nest inhabitants were heavily disturbed by us, did one observe aggressive behavior of *Monomorium* sp. against *C. (K.) micragyne*, which lasted, however, less than one minute.

Discussion

Life conditions and geographic distribution of *Karavaievia*

In the evergreen rainforest zone of Southeast Asia most of the woody plants possess leaves that persist over several years and are not shed synchronously (WHITMORE 1988). Only this type of leaf is suited as a substrate for the long-lasting nest pavilions built by *Karavaievia*. All known *Karavaievia* species nest in this way. Moreover *Karavaievia* workers are able to recognize in advance the moment of natural shedding of individual leaves, possibly through the change of honey dew production of their trophobionts on the decaying leaves within the pavilions (WALDKIRCHER & MASCHWITZ 2002). Consequently, without any loss of colony members such pavilions can be abandoned in time and their brood and trophobionts can be transported to other leaf nests before leaf drop. Synchronous annual defoliation, however, as commonly occurring in woody plants of the monsoon zone during the dry season would simultaneously destroy the numerous pavilions of a *Karavaievia* colony on such a plant, i.e., its whole nesting and trophic base.

Correspondingly, most, i.e., 15 of the known 18 *Karavaievia* species were found in the evergreen rainforest region of Sundaland, i.e., Borneo, Peninsular Malaysia, Sumatra and Mentawai island (DUMPERT & al. 1995). Many of these have been found only once or twice. Only *Karavaievia texens* was found frequently, within a large area ranging from the east coast of Peninsular Malaysia to West Sumatra (DUMPERT & al. 1995 and unpubl.). We suppose that many more species remain undiscovered in the vast unexplored regions of ever wet Sundaland: no collections exist from the moist regions of Java, from large parts of Borneo and Sumatra and from many smaller islands. As *Karavaievia* is neither specialized in living on specific plant species nor in cultivating specific trophobionts and as colony founding queens are able to disperse over water by flight, no limitations by the classical biogeographic Sundaland distribution borders, e.g., such as Wallace's Line, have to be expected (WHITMORE 1988). Thus *Karavaievia* should also be looked for on Sulawesi and on the Philippines.

Three of the species described here have been discovered more than 300 km north of the phytogeographic evergreen rain forest border termed the Pattani-Kangar line (WHITMORE 1988), which is on Peninsular Thailand in the hills of the Khao Sok National Park. This region belongs to the adjoining slightly dryer semi-evergreen rainforest zone, which is still rich in evergreen woody plants. Possibly *Karavaievia* species with their typical life style

occur further northward in the huge range of the monsoon zone of Continental Southeast Asia. In this region we have recently discovered members of two plant-related trophobiotic ant symbiosis complexes, several *Dolichoderus* herdsman symbioses and a myrmecophytic *Macaranga*-ant association (DILL & al. 2002, MASCHWITZ & al. 2004). Though they normally depend strictly on the conditions of the ever wet Sundaland rain forest they are found within the monsoon zone of continental North, especially Central Thailand with its extended dry seasons. Here they have been discovered in moister mountainous regions especially in swampy habitats.

Colony foundation, rareness and high species diversity in *Karavaievia*

As mentioned before most species of *Karavaievia* were found only once or twice indicating their rareness in their habitats. The supposition that colonies are abundant in the inaccessible upper forest canopy is not consistent with our long term observations. We often have found their colonies in lower and middle heights of the forest. Additionally the crowns of hundreds of larger fallen trees checked over many years in our observation area in the Gombak valley/Peninsular Malaysia never were inhabited by any *Karavaievia* colonies. Here in a quantitative counting during a road side clearing action 312 fallen trees up to 12 m height were checked for ants: 12 % of them were occupied by weaver ants (*Oecophylla* or *Polyrhachis* spp.) and 6 % contained carton nests of various ants, but none was inhabited by any *Karavaievia*. During extensive research on nest building behavior, nest architecture and details of nest materials (silk, diverse plant material [carton-nest], and minerals), in tropical canopy-dwelling Formicidae we found clear indication not only for genus specific but even species specific nest constructions (WEISSFLOG 2001). Thus, the majority of free-hanging canopy nests can be assigned to species even without seeing the original inhabitants.

An important reason for the rareness might be the mode of colony foundation of *Karavaievia* species as described here.

The typical mode of colony foundation in *Karavaievia* seems haplometrotic (a single queen establishes a new colony). Because colony-founding queens are not able to build pavilions without silk of last stage larvae, they cannot form any foundation pavilions under free hanging plant leaves. Instead, in at least two species, such queens used as foundation chambers abandoned or weakly colonized leaf nests of other pavilion building canopy ants which still contained trophobionts.

We found colony founding queens of *Karavaievia* in nests of *Monomorium* species (Myrmicinae) which are able to construct their leaf pavilions without silk. This hitherto unknown mode of colony foundation has been found so far in *C. (K.) schoedli* from Thailand and in *C. (K.) melanus* from Borneo. In the cases of *C. (K.) schoedli* and *C. (K.) melanus* the colony founding queen was detected with her own brood and trophobiotic partners inside a single *Monomorium* sp. nest pavilion, while workers of *Monomorium* nested in the neighborhood on the same tree in separate pavilions.

A large colony of *C. (K.) micragyne* from Sumatra mainly inhabited species specific self-constructed pavilions. However, it also had fully taken over some of the typical

pavilions of a canopy dwelling *Monomorium*. Some *Monomorium* sp. pavilions were inhabited by *C. (K.) micragyne* and by *Monomorium* sp. at the same time.

This observation indicates that also in this species colony foundation may happen in a similar way to that of *C. (K.) schoedli* sp.n. and *C. (K.) melanus*.

A similar mode of colony foundation is known from one type of true social parasites, the "temporary social parasites". They have developed a high species diversity in temperate zones but are lacking in the tropics. Like *Karavaievia*, they are rare compared to their host species. Like *Karavaievia* temporary social parasites penetrate into the colonies of their hosts. However true social parasites are different in that they take over not only the nest building but also workers and brood of the host ant colony after having killed its queen. Phylogenetically, true social parasites appear to have evolved directly from their host species or from closely related ancestors. This is the so-called "Emery's Rule" (EMERY 1909).

We do not know whether the *Karavaievia* queens kill the *Monomorium* sp. individuals during the take-over of the *Monomorium* nest pavilions. Nevertheless such a take-over can be classified as a mild sort of interspecific parasitism. However, we do not know whether *Karavaievia* also take over abandoned pavilions of *Monomorium* sp. or nests of other pavilion building canopy ants. Thus questions about whether these relationships are obligate or facultative and whether it is specific or non specific nest founding parasitism, remain open. At present, we can only suppose that the take over of trophobionts is obligate.

More common SE Asian canopy weaver ants like *Oecophylla smaragdina* (FABRICIUS, 1775) or various *Polyrhachis* species need no preformed pavilions and no trophobionts for colony foundation (DOROW & MASCHWITZ 1990, LIEFKE & al. 1998, BUSCHINGER 2001, WEISSFLOG 2001).

The high diversity of *Karavaievia* may be explained by the special biogeographical history of the region and the kind of nesting niche they use. The whole Southeast Asian archipelago has been an extremely dynamic region since Tertiary and especially during Quaternary times (WHITMORE 1988). Geomorphologic events as well as climatic changes, with their extreme sea level changes, caused permanent dramatic processes of land mass splitting and unification, which may have strongly favored isolation and subsequent gene drift and speciation in *Karavaievia* (rarity may also have contributed to such isolation processes). The coexistence of many *Karavaievia* species in small areas with no recognizable niche differences between them indicates that the huge "leave resources in the canopy" are not at all exhausted.

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Zusammenfassung

Es werden fünf neue *Camponotus (Karavaievia)*-Arten beschrieben (Arbeiterinnen und weibliche Geschlechtstiere

aller Arten; Männchen von *C. weissflogi*): *Camponotus (Karavaievia) aureus* DUMPERT sp.n., *C. (K.) hoelldobleri* DUMPERT sp.n., *C. (K.) maschwitzi* DUMPERT sp.n., *C. (K.) schoedli* DUMPERT sp.n. und *C. (K.) weissflogi* DUMPERT sp.n. Ein Schlüssel zur Bestimmung aller bisher bekannten 18 *Karavaievia* wird angefügt.

Soweit bekannt sind alle *Karavaievia*-Arten Weberameisen, die polydome Karton-Pavillions unter oder zwischen Blättern von Holzpflanzen produzieren. Alle Pavillions der volkreichen monogynen Kolonien enthalten Brut und trophobiontische Hemipteren. Kolonien dieses Nesttyps können nur an Pflanzen existieren, die ihre Blätter weder synchron noch häufig abwerfen, d.h. nur an Pflanzen, die hauptsächlich in der immerfeuchten Regenwald-Zone vorkommen. Dementsprechend sind die meisten *Karavaievia*-Arten nur aus der immerfeuchten Regenwaldregion Südostasiens bekannt. Nur wenige leben in den etwas trockeneren, halb-immergrünen nördlicheren *Dipterocarpus*-Regenwäldern. Koloniegründende Königinnen zweier Arten wurden in den Nestpavillions einer Kronenraum bewohnenden *Monomorium*-Art gefunden. Das lässt darauf schließen, dass die Koloniegründung von *Karavaievia* abhängig ist von Nestern Kronenraum bewohnender, Kartonnest bauender Ameisen. Mögliche Konsequenzen dieses Koloniegründungsmodus für die Seltenheit und die Diversität von *Karavaievia* werden diskutiert.

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